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DISTRIBUTION AND SPECIES-FORMING OF ECTO-PARASITES[1]

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I

FOUR years ago I completed, and published in Wytsman's "Genera Insectorum," a catalogue of the Mallophaga (biting bird lice) of the world. This list gives the host distribution of each of the known species and the place or country of capture of the actual host individuals for all cases in which these localities had been recorded. It is, then, a classified list of the known Mallophagan species with their known geographic and host distribution.

I have now in hand, nearly completed, as complement to this already published catalogue, a classified list of all the hosts, bird and mammal, from which Mallophaga have been taken, together with the names of all the parasites recorded from each species, and not only again the actual geographical records of capture but also a statement of the general geographical distribution of each host species. I have determined, for the birds at least, which form the great bulk of the hosts, the synonymy of the various names used for them by the various collectors and reduced them all to the basis of the British Museum Catalogue of the Birds of the World.

By these two lists, namely, the catalogue of parasite

[1] Parts of this paper were read before a general meeting at the Second International Congress of Entomology, Oxford, August, 1912.

species with hosts, and the catalogue of host species with parasites, this group of ectoparasitic insects should be accessible to a wider attention and a more thoroughgoing study from entomologists than it has hitherto had. Indeed the group is deserving of some special attention from general naturalists because of the interesting significance of the conditions of distribution and species forming which obtain in it. It is to the setting out of a few facts and some of the significance concerning distribution and species forming among these insects that the present paper is devoted.

II

The Mallophaga compose a small fairly homogeneous group of about fifteen hundred insect species (as so far known), which pass their whole lives on the bodies of birds and mammals. Those species found on birds are never found on mammals, and those on mammals never occur on birds. Indeed, with exceptions in only two genera, the Mallophaga of birds are of distinct families from those of mammals, the two groups being distinguished structurally by the loss in the mammal-infesting kinds of one of the two tarsal claws, an adaptation connected with the difference between the feathers and hair of the hosts as habitat. Of the 1,500 known Mallophagan species less than one hundred are mammal-infesting, the others all occurring exclusively on birds.

As to the relations of the Mallophaga to other insects I am convinced that they should be treated as a distinct order, finding their nearest affinities in the wingless Psocidæ, such as *Atropos,* the familiar book louse. This relationship is shown not only by similarities in external structure, some of which, however, are only examples of parallelism or adaptive convergence, but by certain more important common characters of internal anatomy, notably a curious pharyngeal sclerite (perhaps the greatly modified hypopharynx), found in both these groups and nowhere else among insects. The habitat and food

habits, also, of the two groups add to the likelihood of the derivation of the Mallophaga if not directly from the Atropidæ, at least from an ancestor that might well have been the common progenitor of both types.

The Mallophaga are all of small size, ranging from 1.5 to 10 mm. in length, with the great majority of them not more than 4 or 5 mm. long and from 1 to 2 mm. in width. The body is much flattened dorso-ventrally, offering an interesting adaptive contrast, in this respect, to the laterally flattened fleas of similar habitat. The body is always wholly wingless, usually strongly chitinized and smooth. The mouth parts are of true biting type, the food being bits of hair or feather or dermal scales, and dried or fresh blood only incidentally and not by a direct breaking of the skin of the host. There are no compound eyes, but a single pair of ocelli placed on the lateral margins of the much flattened head, and the antennæ are from three- to five-segmented, and in about half the genera are capable of being concealed in a small protecting groove on the ventral face of the cheeks. The legs are of normal number, rather long and strong, flattened and fitted for running and clinging. The body is whitish, pale brownish or even dark-brown, often well patterned by blotches or bands of light to black-brown, on the paler ground. These markings almost always indicate specially heavily chitinized portions of the body wall.

The eggs are fastened to the hairs or feathers of the host, and the hatching young are much like their parents in appearance except for their smaller size and paler, unpatterned softer skin. They acquire maturity without any marked metamorphosis. They run freely about from birth, and feed on the hairs or feathers just as their parents do. Neither they nor the adults leave the body of the host except under unusual circumstances. In hen-houses the parasites of the fowls have been occasionally found on the perches or in the nests, but I have often sought carefully, without finding a single parasite, on seaside rocks from which I had just frightened scores of

closely massed resting cormorant, pelicans and gulls, all of them bird kinds whose individuals are practically always well parasitized. When a bird dies or is killed some of its Mallophagous parasites will sometimes wander off of the cold body, but usually they remain on the body and die there within a few days. Before dying they frequently grasp a feather barbule with their strong mandibles and are found there firmly fixed after death.

That they can not live, except unusually, for more than a few days off the body of the warm-blooded host I have proved by keeping them on feathers in ovens at the temperature of the bird body or on feathers in vials next my own body. They die in from two or three to six or seven days off the host body, or on it after death of the bird. It may be that the normal life of the adult Mallophagan is but a week long, but the fact that the young die off the host, or on it after its death, just as soon as the adults, indicates that the parasites are simply unable to live apart from their live hosts, for the only two apparent conditions peculiar to life on a bird's body, namely, a certain constant temperature and feathers for food, are certainly not difficult to reproduce off the body.

At times of actual contact of the bodies of their hosts they undoubtedly migrate from bird to bird. Thus they can move from male to female, or *vice versa* at mating, from mother and father to fledglings in the nest, and from individual to individual of the same species in the case of gregarious birds perching together.

The Mallophaga are, then, true, permanent ecto-parasites, of simple development, some degradation and adaptive modification of body, which occur in the number of one to several species on probably all kinds of birds and mammals, and on practically all bird and mammal individuals, but which, except in special and rather uncommon cases of unusual abundance, cause little serious injury to their hosts. The familiar constant searching of the plumage with the bill by birds is almost always due to the slightly irritating influence of these small para-

sitic insects, but only rarely can this annoyance reach such a pitch as to interfere much with the bird's feeding or resting or sleeping. And the loss of minute bits of feather can certainly be of no consequence at all. The Mallophaga then may be called benignant parasites, as contrasted with the malevolent, blood-sucking fleas and true lice affecting the same hosts.

III

With this fleeting acquaintanceship with the various principal structural and physiological characters of our group of insects, we may attend now to some of the special facts of their distribution and their inter-ordinal relationships, and to the problems which these facts pose to us.

First, with regard to the taxonomic conditions within the group. I have divided the order into two sub-orders, sharply distinguished by certain structural differences whose physiological or ethologic significance, however, is not at all plainly apparent. The most convenient recognition character for this sub-ordinal separation is the condition of the antennæ, short, broad, capitate, three-segmented and concealed in special antennary fossæ in one group; longer, slender, five-segmented, projecting and without receiving fossæ, in the other.

Each suborder contains two families, one of which, with two-clawed members, occurs exclusively (with the exception of one or two species in each of four genera in one case) on birds, and the other, with one-clawed members, exclusively on mammals. Both of the mammal-infesting families include but one genus each; while the two bird-infesting families include fifteen and ten genera, respectively.

The whole order then, with its one thousand five hundred species, comprises but twenty-seven genera, grouped into four families, arranged in two suborders. The disposition of the species among the genera has a rather extraordinary aspect. Nine, or one third, of all

the genera, are represented by but one species each; seven are represented by from two to ten species; three are represented by from twenty to thirty species, three by from forty to sixty-five species, one by one hundred and fifty species, one by two hundred, and three by from two hundred and twenty-five to two hundred and fifty species. Thus while sixteen genera contain less than ten species each, four genera contain more than two hundred species each.

This extraordinary condition of the species in their relation to each other presents an attractive problem. What is its significance? What are indeed the special conditions influencing species-forming within the group?

From many years' work with these insects, including the description of several hundred new species, and the examination of long series of individuals of species in several different genera, I can say with confidence that the evolutionary factor of isolation plays a conspicuous part in Mallophagan species-forming. One soon comes to the acceptance of a very flexible species description for any given Mallophagan kind. While the score of individuals of one kind that one may collect from a single host individual will agree well with each other as to details of structure and pattern, the specimens of the same kind from another host individual of the same host species collected either in the same locality or a distant one, and the specimens from a third host individual and from a fourth and fifth, and so on, will all show many obvious, if mostly small, variations from the specimens taken from the first or any other host individual.

That is, each host individual is, in a way, a small island, biologically considered, with its inhabitants more or less nearly completely isolated from the inhabitants of other host islands. So that each species is made up of many dislocated small groups which may have, as when they are on birds of solitary habit, but little opportunity for mixing and cross-breeding with the members of the species-body as a whole. The group on one host bird may

meet the group on the mate of this host, and these two mingling groups may send their representatives or their offspring to the young of the two mated hosts. But that is about the extent of their participation in the life and character of their species as a whole, and it is an extent which plainly must result in the establishment of an hereditary strain characterized by the special slight structural idiosyncrasies peculiar to the few ancestors from which the strain takes its origin. In the case of the parasites of more gregarious bird kinds, as the seabirds that mass for rest or brooding on ocean rocks or shore cliffs, or the swallows and swifts that live in colonies in caves and chimneys, or those gallinaceous birds like the partridges of California that gather in close bands of two or three score individuals, or others of any kind of similar habit which may give chance for repeated actual personal contact of body with body sufficient to permit of migration of the wingless but active parasites from bird to bird, this element of isolation is less accented. But it still plays an important figure. For both the winglessness and the manifest stay-at-home habits of the parasites make their movement from host to host at best a desultory and almost accidental one.

This combination of conditions, then, may serve to explain partly both why each species must be given a very flexible description and why one might describe and name, if he liked, many varieties of each species; and it explains, in some measure, why there are a good many species in the order, and why there are many in each of a few genera, although it does not explain, perhaps, why there are some genera with very few, and indeed even, so far as yet known, single species.

The explanation of the actually small number of genera and families depends, I think, upon one of the conditions in the life of the Mallophaga which is directly opposed, in its influence, in a way, to the isolation condition making for a variation that results in numerous varieties and species. It is this. Although the different host species

may differ much among themselves as to habitat, habits, plumage markings, etc., yet as places of residence and providers of food for their external parasites they are all much alike. The temperature is the same, the feathers as food are about the same. Although the parasite's host may live in the water, the parasite itself, safely tucked away next the skin or among the feathers, lives on dry land in free air, for the water, even where it continually covers part of the plumage, as in swimmers, or occasionally all of the plumage, as in divers, only touches the plumage surface. Beneath this surface it is always dry and there is always free air.

Thus despite an isolated life for the inhabitants of each host island, and the great variety of these islands as regards name and relation to phyletic mainlands, the actual life conditions are monotonously alike on all these islands. So that there is, for the Mallophaga, no such variety of conditions of habitat and food and food-getting and mate-seeking and egg-concealing and young-rearing as would tend sharply to select and promote variations, with a result of genus and family making. There is no external influence at work promoting wide divergence. The generic and family distinctions tend to be few; the varietal and specific tend to be many.

IV

As a direct outcome of these conditions of life of the Mallophaga there arises an extremely interesting state of affairs concerned with their host and geographic distribution, a state of affairs which reveals, I think, a principle or fundamental consideration concerning the distribution of wingless ecto-parasites in general. This special subject may be introduced by a swift résumé of our present knowledge of the facts of the distribution of the Mallophaga. In this résumé I include some particular illustrations, by examples, of certain special distributional conditions.

As Mallophaga have been taken so far from but a

hundred species of mammals, representing 48 genera, 24 families and 5 orders, any special scrutiny of the conditions of their distribution among mammalian hosts would hardly be worth while. But such scrutiny can certainly now be advisedly undertaken as regards the distribution among birds. For the Mallophagan host list includes already more than 1,100 bird species, representing 33 of the recognized 35 orders of living birds. The known living bird species number, according to the British Museum Catalogue, about 18,500. This catalogue, I should note, elevates to the position of species, or at least to the seeming of species, by cataloguing them binomially, the so-called varieties or trinomially dubbed subspecies of the continental and North American ornithologists; and I have followed this custom in my list—although against my belief in its taxonomic implication—for the sake of having a common and universally accessible basis for the host names.

Thus one out of every seventeen known living bird species is now included in the Mallophagan host list, as are 625 out of the 2,700 recognized living bird genera, and 120 out of the 160 living bird families. As comparatively few bird kinds are still unknown, and as on the other hand only a good beginning has been made in finding and describing the Mallophagan kinds, it is certain that the list of hosts of these parasites will increase rapidly in proportion to the total number of bird species. From the proportion of the number of different bird hosts parasitized by each Mallophagan species and the proportion of bird families and genera already in the host list, I estimate, roughly, the total number of living Mallophagan species to be about 5,000.

From the three Acarinate or Ratitian bird orders, namely, the Rheiformes, or South American rheas, the Casuariiformes or Australian cassowaries, and the Struthioniformes or African ostriches, only five species of Mallophaga have so far been recorded. On the rheas occur three species of *Lipeurus,* one being found on each

of two host species and the other two on a third. On one species of Australian cassowary are found two Mallophagan kinds, one of which is the same species as that found on two of the South American rheas, while from the African ostrich, *Struthio camelus,* are recorded two parasite species, one of which is the same as that found on the third rhea. Here, at the very outset, is a remarkable case of distribution. Identical parasitic species on hosts as widely separated, geographically, as Australia and South America and Africa, but hosts all of a certain degree of genealogic affinity.

The order Tinamiformes, the tinamous of South America, curious birds, rather pheasant-like but presumably not really pheasants nor true Galliformes of any kind, is represented by eleven species in the Mallophagan host list. Most of these tinamous are well parasitized, a species of *Nothura* having four parasite species, one of *Crypturus* five, one of *Tinamus* six, one of *Rhynchotus* eight and another of *Tinamus* even nine parasite species representing five genera, of which two are peculiar to the group. Of the other Mallophagan genera found on the tinamous two that specially characterize the pheasants and other gallinaceous birds are, by odds, the most commonly represented. And this condition suggests another interesting problem. Is it going to be possible to get suggestions regarding the phyletic affinities of hosts from the character of their parasitic fauna? Take, for example, an order of birds troublesome to the ornithological taxonomists. Will the evidence of the presence on members of this order of certain parasitic genera characteristic of another order indicate their affinities to this second order? It does indeed seem, in the case of the Tinamiformes and Galliformes, as if the evidence from the Mallophagan distribution was in conformity with that suggested by certain structural similarities in the two groups.

The great order Galliformes, including the pheasants, partridges, quail, etc., is represented in the host list by

seventy-eight species, from which are recorded about 150 Mallophagan species representing six genera, two of which, *Goniodes* and *Goniocotes,* are the most abundantly represented and occur much more commonly on birds of this order than those of any other unless it be the Tinamiformes, just spoken of. The other Mallophagan species recorded from the Galliformes belong to the large genera *Lipeurus, Colpocephalum* and *Menopon* which include species from most bird orders. The Mallophagan genus *Docophorus,* the second largest of all in the matter of number of species, and abundantly represented on almost all other bird groups, is totally unrepresented on the Galliformes. The Gallinaceous birds are, as a rule, strongly parasitized both as regards number of Mallophagan species and number of individuals. One of the brush-turkeys, *Megapodius,* has ten parasitic species, the painted Chinese pheasant has nine, and the Texan quail, eight. The domestic fowl has twelve Mallophagan species and its reputed ancestor, the wild Indian jungle fowl, *Gallus bankiva,* four, all of which occur on its domesticated descendant. The Mallophagan species *Lipeurus variabilis* is common to nine different hosts of the family Phasianidæ.

The small order of so-called pigeon grouse, the Pteroclidiformes, has two species in the host list, each parasitized by the single Mallophagan species, *Nirmus alchatæ,* not found on other birds. The two hosts species have overlapping geographic ranges.

The Columbiformes, or doves and pigeons, are represented in the host list by 40 species. The Mallophagan genera *Goniodes* and *Goniocotes,* so common also on the pheasants and tinamous, are very well represented among the pigeon parasites. The single Mallophagan species *Lipeurus baculus* is recorded from nineteen of the forty pigeon host species, whose geographic distribution includes Europe, Asia, Africa, North America, Malaysia, Australia, Madagascar and the Galapagos Islands. The European-Asiatic rock dove, *Columba*

livia, immediate ancestor of the domestic pigeon, has two Mallophagan parasites of which one, the wide-spread *Lipeurus baculus,* is found on the domestic pigeon. The other species, *Goniocotes compar,* is common to several other wild doves, but, curiously enough, it has not been recorded from the domestic pigeon. The isolated Galapagos Island dove, *Nesopelia galapagoensis,* peculiar, both in genus and species, to these islands, is parasitized by *Lipeurus baculus,* and by four other Mallophagan species not found on any other pigeons.

From the hoazin, strange aberrant bird of the Amazon forests, and single representative of the order Opisthocomiformes, I have recorded three Mallophagan parasites, two of them new species, and one a member of the genus *Goniocotes,* a genus rather characteristic of the pheasants and pigeons. It is exactly to the pheasant-like birds that ornithologists seem at present inclined to associate this lonely South American bird.

The Ralliformes, or rails, gallinules and coots, are represented in the Mallophagan host list by twenty-three species. One small genus of parasites, *Oncophorus,* is almost limited to the order. The old world coot, or mudhen, *Fulica atra,* has seven Mallophagan species representing six genera. Its congeneric sister species of the new world, *Fulica americana,* has twelve Mallophagan species, of which five are identical with those found on the old world coot. The parasite species *Oncophorus bisetosus* occurs on six different rails, three of them North and Central American and three of them Malaysian and Australian.

The Podicipedidiformes, or grebes, are represented in the host list by six out of the 25 known species of the order, from which are recorded eight Mallophagan kinds. On five of the six grebe species occurs the Mallophagan species *Menopon tridens,* found elsewhere also on certain loons, auks and ducks. The six grebes are geographically distributed as follows: two new world, three old world, and one circumpolar.

Seven species of Mallophaga have been taken from four species out of the known five of the order Colymbiformes or loons, one of which is limited to the old world with three circumpolar in range. On three of these loons occurs the Mallophagan species *Docophorus colymbinus,* and *Nirmus frontalis* is common to two, and *Menopon tridens* to two. But the continuity of geographical range among the loons does not seem to have produced any special effect of commonness of parasites to different host species. In the preceding order, for example, that of the grebes, there is more commonness of Mallophagan species, although at the same time more isolation of the hosts geographically.

From two penguins representing the order Sphenisciformes, three Mallophagan species have been recorded. Two of these belong to the genus *Goniodes,* a genus best represented among the pheasants and pigeons. The third is type-species of a genus so far not elsewhere recorded.

The Procellariiformes, or petrels and albatrosses, of which about a hundred living species are known, are represented in the host list by thirty-two species, and give evidence of being a strongly parasitized group of birds. Ten Mallophagan kinds have been taken from one species of *Puffinus,* nine from another, eight from another and seven from a fourth. Besides these, four other species of *Puffinus* are in the host list. On the four *Puffinus* species most infested there is one parasite kind common to all, and four parasite species common to three of them. Six species of albatrosses, genus *Diomedea,* are included among the Procellariiform hosts. On five of them occurs the giant Mallophagan species *Lipeurus ferox,* 10 mm. long, and on five also the large, broad species *Eurymetopus taurus.* Nine species of Mallophaga have been recorded from the single albatross species *Diomedea albatrus,* of the North Pacific Ocean. Four Mallophagan genera, each of them containing but a single species, are peculiar to the order. The birds of

this order range the great oceans in overlapping zones and reaches.

The order Alciformes, including 29 known living species of auks, murres and puffins, is represented in the host list by sixteen species which are parasitized by sixteen Mallophagan species belonging to but two genera, *Docophorus* and *Nirmus,* with the exception of one species of *Menopon.* These two genera are, however, not at all limited to the Alciformes, but are two of the largest and most widely distributed of the Mallophagan genera. *Nirmus citrinus* occurs on four Alciform hosts, and *Nirmus maritimus, Docophorus celedoxus* and *Docophorus montereyi* on three each. *Nirmus pacificus* and *Docophorus atricolor* occur on two each.

The homogeneous order Lariformes, or gulls and terns, including 122 known living species, is represented by fifty species in the host list, of which two dozen belong to the gull genus *Larus,* and one dozen to the tern genus *Sterna.* Gulls and terns are strongly parasitized. Thirteen species of Mallophaga, representing four genera, have been recorded from *Sterna fuliginosa,* and ten species from the tropical noddy, *Anous stolidus.* The gull and tern parasites are mostly of the genus *Docophorus* and *Nirmus* with some *Menopon* and *Colpocephalum* and a few *Lipeuri. Docophorus lari* occurs on nineteen species of *Larus,* and *Nirmus bilineolatus* on eleven. *Docophorus melanocephalus* occurs on four species of *Sterna.* Many of the members of this bird order range widely, but some are limited to new world or old world shores.

The large order of waders and shore-birds, the Charadriiformes, is represented in the host-list by sixty-three species. The Mallophagan genus *Nirmus* is especially commonly met with on these birds, and has many species characteristic of them. From the cosmopolitan sanderling, *Arenaria interpres,* with its individuals from old and new world meeting in high latitude breeding grounds, fourteen Mallophagan species have been recorded, of which six are *Nirmi.* Ten Mallophagan kinds

occur on the European curlew, *Numenius arquata,* of which one occurs also on the new world curlew, *Numenius longirostris.* It is the only Mallophagan so far recorded from this host. *Hæmatopus galapagoensis,* limited to the Galapagos Islands, has three Mallophagan species, of which one is peculiar to it, one is a duck-infesting species, probably a normal straggler under conditions which I shall explain later, and one is a form found also on *Hæmatopus ostralegus,* the common oyster-catcher of Europe, Central Asia and Africa. The old world avocet, *Recurvirostra avocetta,* has six Mallophagan species, while the new world avocet, *Recurvirostra americana,* has four, of which two, *Nirmus pileus* and *Nirmus signatus,* are common to both hosts. The other two are new. Two species of the curious aberrant Charadriiform family Parridæ occur in the host-list, each having but a single Mallophagan species, and that the same for both hosts. One of the host species is limited to Australia, while the other ranges from India to the Malay Peninsula.

The Gruiformes, or cranes, thirty-four living species, are represented in the host-list by twelve species, parasitized by twenty Mallophagan kinds. The herons and egrets, order Ardeiformes, are represented by forty-five species. *Lipeurus leucopygus* occurs on both the old world bittern, *Botaurus stellaris,* and the new world one, *Botaurus lentiginosus.* It occurs also on two other herons, both old world species. From *Butorides sundevalli,* peculiar to the Galapagos Islands, I have had four species, all previously described by me from various maritime birds of the Pacific. This is a case of straggling, but as I shall point out later in connection with the conditions shown by certain other Galapagos Island hosts, a case of what may be called normal straggling, unusual on the whole, but possible and especially common in the case of Galapagos, and perhaps other, island hosts.

The Palamedeiformes, or South American screamers, are represented in the host-list by two species, parasitized by three Mallophagan kinds. One of these is com-

mon to both hosts. The flamingoes, constituting the order Phœnicopteriformes, are parasitized by four species of Mallophaga of four different genera.

The Anseriformes, swans, geese and ducks, are represented in the host-list by sixty-four species, seven being swans, nine geese and the rest ducks. The swans have a Mallophagan genus, *Ornithobius,* peculiar to them, which occurs on four out of the seven species. The species *bucephalus* of this genus occurs on two old world and one new world species. Six of the seven swan kinds belong to the genus *Cygnus.* Three of these are old world, two new world and one circum-polar in range. *Trinoton conspurcatum* has been recorded from the three old world and the single circumpolar species, and *Docophorus cygni* from two old world and one new world species. *Cygnus cygnus* of Europe has six Mallophagan species. The curious Australian swan *Chenopsis atrata* has two parasite species neither of which occurs on any other swan. Among the geese are three species of *Anser,* two of them old world and one new world, with the parasite *Lipeurus jejunus* common to them all, and four species of *Branta,* one of which also carries *Lipeurus jejunus.* This Mallophagan species also occurs on the domestic goose. The forty-four species of ducks of the list are parasitized by forty-two species of Mallophaga. Of these, *Docophorus icterodes* is recorded from eleven duck species, *Lipeurus squalidus* from fifteen and *Trinoton luridum* from nineteen, these duck kinds including African, Asiatic, European, North American, South American and cosmopolitan species. A duck kind from Australia and Malaysia has four parasitic species, all peculiar to it. Three species of ducks have the three most familiar duck-infesting Mallophaga, mentioned above, common to them all. *Anas boschas,* the ancestor of the domestic duck, has these three and just one more. But so far only one of the three has been recorded from the domestic duck. While many species of ducks, and most individuals of the species, are parasitisized, it is rare that more than two

or three or four—the maximum is actually six—Mallophagan species are found on a single host species. The great bulk of the parasitization comes from comparatively few Mallophagan species, notably the three species already named.

The Pelecaniformes, 75 living species, including the pelicans, cormorants, boobies, man-o'-war and tropic birds, are represented in the host list by thirty-three species. Thirteen of these are cormorants of the genus *Phalacrocorax,* and nine are boobies of the genus *Sula. Lipeurus setosus* occurs on two African and two Australian and Malaysian species of *Phalacrocorax. Lipeurus toxoceros* occurs on one cosmopolitan cormorant and on two others, one of South and Central America and one of North America. *Lipeurus faralloni* is recorded from three North American west coast species. Five species of *Pelecanus,* three new world and two old world, are included in the list. *Menopon titan* occurs on two of the new world and one of the old world species, *Lipeurus bifasciatus* on one new world and both of the old world forms, and *Lipeurus forficulatus* on two new world and one old world species. Eleven species of Mallophaga are recorded from the cosmopolitan man-o'-war bird, *Fregata aquila,* and eight from the beautiful white tropic bird, *Phaeton æthereus.*

The Cathartidiformes, or new world vultures, are represented in the host list by four species. There are but nine species in the order. The four species in my list are the great condor of the Andes, ranging from Patagonia to Ecuador; the great king vulture of the northern Andes, Central America and Mexico; the rare Californian condor of northern Mexico, Baja California, and California north to its middle region; and finally, the ubiquitous turkey vulture, smaller and far more abundant than any of the others, that ranges over all of North America and, in winter, gets into northern South America. Thus the ranges of the four species combined extend the whole length of the western coast of the new

world. And although each bird has its own stretch of coast mountains, the range of each overlaps that of some other. The individuals of all these bird species, except the last named, are few and solitary in habit, resting and nesting in inaccessible mountain places, but meeting a few of their kind occasionally at common table around some dead or dying animal. Turning now to the parasites of these lonely birds, we find one species, the well-marked, rather large *Lipeurus assessor* common to all four vulture species. But *assessor* has been taken from the wide-spread turkey vulture only in Panama, *i. e.*, within the range of the king vulture. *Læmobothrium delogramma* is also found on both the king and the turkey vultures, but has been taken from the latter host again only from Panama specimens. The king vulture and Californian condor, whose ranges overlap in Mexico, have one parasite species, *Menopon fasciatum,* common to both. These are the only cases of commonness of Mallophagan species to two or more of these great vulture kinds. And all are pretty well parasitized, seven Mallophagan species being recorded from the king vulture, five from the South American condor, five from the North American turkey vulture, and two from the Californian condor. It is well to keep in mind, in noting this rather abundant parasitization, that the feeding habits of the birds give some opportunity for the straggling of parasites from other bird or mammal kinds, serving, in the persons of moribund or just dead individuals, as prey. It is therefore indeed important to note that no mammal-infesting Mallophaga have been taken from any vulture, despite the excellent chances for such straggling. Perhaps the difference between a mammal and a bird host is too great to permit a parasite adaptively specialized for life on one to persist successfully on the other. Or perhaps there is a physiological antipathy, a negative chemotropism, too strong to permit the straggling. Yet I recall that in my days as a bird-collector and maker of skins, I repeatedly had the annoyance of discovering

that I was a temporary host for individuals of parasites more normal to a duck or a barn owl than to man! But these wanderers seemed as anxious to leave their chance-found new host as was the host to be relieved of them; a few moments was the usual extent of their stay.

This point of the reluctance of Mallophaga to migrate, even with good opportunity, from normal or characteristic host, to another, is emphasized when we come to examine the parasitic conditions of the next bird order, the Accipitriformes, or falcons, hawks and eagles, almost all species of which capture living mammals of one kind or another. In the parasitic records of the seventy species of this order included in my host list, there is not a single record of a Mallophagan species of either of the strictly mammal-infesting genera, and there are but three or four records of bird-infesting species that are plainly stragglers from prey, as is, for example, a typical duck parasite recorded from an American hawk, and a pigeon parasite from a European falcon. In fact, the Mallophagan species taken from the birds of prey are about as characteristic of their host-group as are those of any other group, although there are, indeed, no parasitic genera wholly peculiar to the birds of prey. The Mallophagan species *Colpocephalum flavescens* is found on twenty-one Accipitrine species and *Nirmus fuscus* on eighteen, the hosts representing species from all parts of the world, including, for *Nirmus fuscus,* at least, Australia. They represent, too, most of the principal families and subfamilies of the order. *Colpocephalum flavescens* is found on *Thrysaëtos,* a new world eagle genus, on *Gypaëtus,* an old world eagle, and on one cosmopolitan species of *Aquila* and one old world *Aquila.* The eagles, like the great vultures, are characteristically solitary birds, only the members of each household, that is, male, female and young, coming into contact with each other. They are typical host islands. Some of the birds of prey are strongly parasitized, as the golden eagle, *Aquila chrysaëtus,* with

nine Mallophagan species, and the South American caracara, *Polyborus tharos,* with eight.

In the Strigiformes, or owls, represented in our host list by nineteen host species, we have added confirmation of the Mallophagan hesitancy to straggle even with good opportunity. There is no record of a mammal parasite on any owl, nor but two or three of Mallophagan species characteristic of birds of other orders. Of the characteristic owl parasites, *Docophorus cursor* occurs on all three species of *Asio* included in the host list. One of these Asios is restricted to the Galapagos Islands, one ranges Mexico and temperate North America, and one occurs in both old and new worlds. The genus *Strix,* barn owls, is represented by two species, one the old world barn owl and the other the barn owl of temperate North America. The Mallophagan species *Docophorus rostratus* occurs on both of them. *Asio accipitrinus,* the cosmopolitan hawk owl, carries seven Mallophagan species.

The Psittaciformes, parrots and cockatoos, are represented in the host list by twenty-eight species, infested usually by only one to two or three parasite kinds, although five have been recorded from a Senegambian *Psittacus.* It is pleasant to note that the cruel New Zealand Keas, which have adopted the extraordinary habit of alighting on the backs of living sheep and tearing their flesh, even through to the vitals, have at least three Mallophagan parasite species to make life a little uncomfortable for them. One of these species, *Lipeurus circumfasciatus,* is recorded from three other parrots of Australia and Malaysia.

The catch-all order Coraciiformes, including the rollers, kingfishers, hoopoes, mot-mots, poor-wills, swifts and humming-birds, is represented in the list by forty-five species, of which six are kingfishers, six are hummers and five are swifts. Of the five swifts three are of the new world and two of the old. The Mallophagan genus *Nitzschia* is peculiar to the swifts and is found, repre-

sented by four species, on all five in my list. *Nitzschia pulicaris* is found on one old world and two new world species. The humming-birds are not badly parasitized, although three Mallophagan species have been recorded from a single one of these tiny host kinds. They are especially infested by the Mallophagan genus *Physostomum*, although species of this genus occur on several other passerine bird hosts.

The trogons, order Trogones, are represented in the host list by two species, infected by two Mallophagan species, both of the genus *Nirmus*. The Coccyzes, or cuckoos, represented by twenty-three species, have usually but one, although sometimes two or three Mallophagan kinds to a host species. And this condition of slight parasitization is also true of the five species of toucans and barbets, order Scansores, included in the list. *Docophorus latifrons* is recorded both from the common European cuckoo and, in varietal form, from the common American cuckoo.

The order Piciformes, the woodpeckers, is represented in the list by twenty-six species, each carrying but one to two or three Mallophagan kinds to its discredit. The woodpecker genus *Dendrocopus* is represented by six species of which five belong to the new world and one to the old world. *Docophorus superciliosus*, described from the old world species of *Dendrocopus*, occurs also on one of the new world species and also on another old world woodpecker of different genus. One of my Western American Mallophaga species occurs on three woodpecker kinds in California, one in Baja California and three in Costa Rica. It seems to be a pervasive parasite of American West Coast woodpeckers. Of the seven host species from which it is recorded three belong to the one genus *Melanerpes*.

The order Eurylæmiformes, or Malayan broadbills, is represented in the host list by one species parasitized by two species of Mallophaga, while the order Menuriformes, the beautiful lyre-birds of Australia, three living

species, is also represented by one species, parasitized, however, by six Mallophagan species all peculiar to it.

This brings us to the last bird order of our list, the great group of Passeriformes, the perching and singing birds, with its various familiar families of flycatchers, swallows, wrens, thrushes, titmice, warblers, larks, finches and sparrows, tanagers, blackbirds, crows and jays, *et al.* It contains 5,000 known kinds, but is represented in our host list by but three hundred and eight species, divided among more than a score of families. Practically no Mallophagan species found on members of this order occur on birds of any other order. Two Mallophagan kinds have a wide host distribution within the order. *Docophorus communis* has a host list of one hundred and thirty Passeriform species, of which thirty-eight are members of the family Fringillidæ, this being more than half of all the Fringilline birds from which Mallophaga have so far been recorded. These one hundred and thirty hosts of *Docophorus communis* represent most of the families of the Passeriformes and, in their geographic distribution, all of the principal regions of the world. A score of varieties have been named within the species, and a score more might be. But this would be to say no more than that there is a wide variation among the members of the species, and to attempt to make categories of this variation is really labor lost. This large variability of *Docophorus communis* is simply the most conspicuous example within the order of that condition of persistent variation, due chiefly to isolation, that I spoke of at the beginning of this paper as a condition occurring in almost all the Mallophagan species; a variation fostered by isolation, unrestrained by cross-breeding, but not specially emphasized by adaptive modification, nor sharply selected for life and death value.

Another Mallophagan species widely spread among Passeriform hosts is *Nirmus vulgatus,* a species described by me several years ago and which I have so far taken

from forty new world host kinds, including several genera and species peculiar to the Galapagos Islands. All the specimens from Galapagos Island hosts show a number of small but obvious distinguishing characters, and I have given them the varietal name *galapagoensis*. This constant distinction would indicate that the Galapagos individuals, though now infesting several different host kinds, are all descended from a single original introduction of the species; or that there is some external modifying condition of life on Galapagos Island birds that would produce a convergence among the descendants of ancestors representing several introductions, a supposition hardly tenable, especially in the light of the peculiar life conditions of the Mallophaga.

The Passeriform family Tyrannidæ, the new world flycatchers, is represented in the list by eighteen species parasitized by two Mallophagan species, of which but two, one being *Docophorus communis,* are recorded from old world Passeriform hosts. Although this family has a continuous geographical distribution over North, Central and South America, there is no unusual commonness of parasitic distribution in it. No one Mallophagan kind occurs on more than two flycatcher species, except in the Galapagos islands, where *Nirmus vulgatus* var. *galapagoensis* is found on all three of the flycatcher kinds occurring there. All the other Mallophagan species on these Galapagos flycatchers are forms restricted to the islands, although not to the flycatchers.

The swallows, Hirundinidæ, are represented by ten species of which two are old world, five new world, two both old and new world, and one from the Galapagos Islands. From them are recorded twenty Mallophagan species, of which *Menopon rusticum* is found on one old world, one new world, one old and new world, and one Galapagos Island host. *Docophorus excisus* is found on one old world and two new world hosts, and *Nirmus longus* on two new world and the two old and new world hosts. Seven Mallophagan species have been taken from

the Galapagos Island swallow, of which one is found on two new world swallows and one is the *Menopon rusticum* already mentioned as common to one old world, one new world and one old and new world host.

Mallophaga have been taken from three species of wrens, Troglodytidæ, of three different genera. Two species of parasites have been taken from each host species, and no one of these Mallophagan species occurs on more than one host kind.

The Cinclidæ, or dippers, are represented in the list, by two species of *Cinclus,* one from the old world and one belonging to the new. One Mallophagan species, a *Menopon,* is common to both hosts, and each host species has, in addition, another Mallophagan species, a *Docophorus* in one case and a *Nirmus* in the other.

The Mimidæ, or mocking-birds, are represented by seven species, of which five belong to the genus *Nesomimus* peculiar to the Galapagos islands. The other two are North American. There is one Mallophagan species on each of the American mockers, and from one to as many as eight on the various Galapagos Island hosts. But the Mallophaga of the Galapagos Island mockers are mostly species common to numerous other birds of the islands, some of these birds being widely separated phyletically from the Mimidæ. For example, the characteristic *Lipeurus baculus* of the pigeons has been taken from one of the mockers. This apparently abnormal condition has a normal explanation that we shall take up in connection with certain still more conspicuous examples of the anomalies among the Galapagos records.

The Turdidæ, or thrushes, are represented in the list by twenty-three species. *Docophorus communis* occurs on nine of them. *Menopon thoracicum* is recorded from the old world *Turdus viscivorus* and from *Merula grayi* and *Catharus gracilirostris* from Costa Rica. The Sylviidæ, or old world warblers, are represented by five species, on four of which *Docophorus communis* is the only parasite. The Ampelidæ, or waxwings, are represented by four

species, two of which are North American, one Central American, and one common to both old and new worlds. *Docophorous communis* and *Nirmus brachythorax* occur on three of the four species.

Mallophaga have been recorded from eight species of Laniidæ, or shrikes, of which three are old world species, three new world and two are Australian. *Docophorus communis* occurs on five of the old and new world species, but not on either of the Australian hosts. Four of the eight species belong to the genus *Lanius,* three being new world and the other an old world species. *Docophorus communis* occurs on them all.

The Paridæ, or titmice and chickadees, are represented in the host list by eleven species, four old world and seven new world. *Docophorus pari* is recorded from three old world species of three different genera. *Docophorus rutteri* occurs on two new world species of the same genus and the same geographical region. Mallophaga have been taken from three kinglets, family Regulidæ, two of them old world species and one new world. *Physostomum frenatum* is recorded from one old world and one new world host species.

The rather large family of Mniotiltidæ, or wood-warblers, is represented by twelve species, three of them from the Galapagos Islands, and the others from North, Central and South America. *Docophorus communis* is the only old world Mallophagan species occurring in the group, being found on three of the American host species.

The Drepanidæ, or honey creepers of the Hawaiian Islands, are represented in the list by three species of three different genera. Seven Mallophagan species, all except one peculiar to the host group, have been taken from these three hosts. One of the Mallophagan species is common to all three.

Mallophaga have been taken from five species of Alaudidæ, or larks, three of them old world, one new world, and one inhabiting both old and new worlds. *Docophorus communis* occurs on four of the lark species.

Only three other Mallophagan kinds have been recorded from the family.

The great family of sparrows and finches, the Fringillidæ, including nearly 1,200 bird kinds, is represented in the host-list by seventy-six species. The Mallophagan species *Docophorus communis* has been recorded from thirty-eight of these from the old and new worlds, and *Nirmus vulgatus* from eighteen, all from the new world. There have been almost no Mallophagan records made from old world hosts since I described *vulgatus,* which is possibly the explanation of the lack of any old world records for it, although it may really be that the species does not occur in[2] Europe. Among the Fringilline hosts of the Mallophaga there are nine species representing two genera, *Camarhynchus* and *Geospiza,* peculiar to the Galapagos Islands. Most of these nine host species are pretty strongly parasitized, one of them, indeed, *Geopiza fuliginosus,* having had nineteen Mallophagan species taken from it, the record as regards number of parasite species from a single host form. Of these nineteen Mallophagan species, four belong to the genus *Docophorus,* five to *Nirmus,* five to *Lipeurus,* two to *Colpocephalum,* two to *Menopon,* and one to *Goniocotes.* Among them are included all of the seven species that have been recorded from *Camarhynchus pallidus,* the most parasitized species of this sister sparrow genus peculiar to the islands. But also there are included several Mallophagan species found on various other host birds widely separated phyletically from *Geopiza* and *Camarhynchus.*

In fact, in studying the parasitization of the Galapagos Island birds—and I have had in hand two very full collections from them—one is struck by the breakdown of the general rule that the Mallophaga of one host group, as a genus or family or order, shall be more or less nearly exclusively confined to members of the group, and hence to be characteristic of it. For example, one does not expect to find the abundant duck parasite, *Trinoton luri-*

[2] I have recently recorded *Nirmus vulgatus* from a starling from Egyptian Sudan.

dum on pigeons, nor the familiar pigeon parasite, *Lipeurus baculus* on ducks, and one does not so find them. Nor to find on sparrows or hawks Mallophaga of the genera *Ancistrona, Eurymetopus* and *Philoceanus,* characteristic of maritime birds; nor on owls or cuckoos to find certain maritime bird-infesting species of *Lipeurus* and *Docophorus,* genera in themselves represented by species on hosts of many orders. But in the two carefully made collections of Mallophaga from the Galapagos Islands, representing in their host lists practically all the bird species known to inhabit the islands, I have noted the exception to be the rule. And from interviews with the collectors—one of them was one of my own assistants—I have determined the probable reason for this unusual state of affairs. It is this. The birds of the land, the birds of the shore, and the birds of the sea meet and rest side by side on the shore rocks and sands. The land birds live chiefly not in the dense, almost impenetrable jungle of the interior of the islands, but in the outer or shore fringe of it. Here they meet and mingle with the hosts of sea birds that find resting and nesting ground on these few small bits of solid earth set in the midst of all the leagues of inhospitable moving waters that constitute their range. This brings about the opportunity and the reality of an abnormal but natural straggling, which results in an extraordinary and probably unique host distribution of the parasites. And thus it is that the little Galapagos Island sparrow, *Geospiza fuliginosa,* comes to be the bearer of more Mallophagan species than any other bird in the host list and has included among its guests many that more rightfully belong to birds of ocean and shore sands.

The Tanagridæ, or tanagers, are represented in the host list by ten species. *Menopon thoracicum* is common to four of them, all of Central American range. The Icteridæ, including the blackbirds, grackles, meadowlarks, and American orioles, are represented by twenty-two host species, and the Sturnidæ, or starlings, by seven.

The Paradiseidæ, the radiant birds of paradise, are represented in the list by eight species.

Finally, the Corvidæ, or crows and jays, are represented at present by thirty-two species, about one out of ten of the known kinds, of which thirteen belong to the genus *Corvus*. Both these numbers will be increased when I am able to incorporate in the list the records, already worked but not yet published, of a considerable collection of Mallophaga from the crows and jays of India, sent to me by Superintendant Annandale of the Indian Museum at Calcutta. The Corvidæ are provided with a number of parasite species characteristic of the family, such as *Docophorus atratus, Colpocephalum subæquale, Menopon mesoleucum, et al.* This latter parasite occurs on four species of *Corvus*, two of old world and two of new world range. *Colpocephalum subæquale* occurs on two North American and one European species of *Corvus*.

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From these examples of Mallophagan distribution illustrating various special conditions of host relations a number of rather important points of significance appear. Of two only, however, which indeed at bottom are really one, shall I speak. First, there is apparent in Mallophagan distribution a general faithfulness of parasite to host kind or group of related host-kinds, and this without much reference to geographical conditions. And second, there appears a plain tendency for a single parasite species to be common to two or more related host species, even though these hosts be so widely separated geographically and so restricted to their separate geographic ranges that all possible chance of contact between individuals of the different host species seems positively precluded. The American and the European avocets do not meet; nor do the American and European coots. Yet the two coots have five Mallophagan species in common, and the two avocets two. The American and European bitterns are both infested by a common parasite species.

The American and old world dippers or water ouzels are in the same case. The same Mallophagan species occurs on both an old world and a new world kinglet. One parasite species is common to two old world and two new world crows. Practically all of those isolated bird species found only on the Galapagos Islands are infested by Mallophaga that occur on related new world or even old world hosts.

Now, removing all cases of even an imaginable rare possible contact of bodies between these related but specifically distinct hosts, such as might occur in birds of circum-polar range, or in gregarious maritime kinds meeting on common mid-ocean islands, or in kinds occasionally exported by man from their normal range, etc., and there are still left many cases of this commonness of a parasite species to two or more usually rather closely related host species of quite distinct geographic range. How can this actual condition be explained?

I can see but one answer. That is, that the parasite species has been handed down practically unchanged to the present specifically and even generically distinct several bird species from their common ancestor of earlier days. The parasite species dates from the days of this ancestor. With the splitting up of the ancient host species due to geographic wandering and isolation of groups of its individuals, and their gradual divergence in plumage, color and pattern, shape of bill or toes or wings, caused partly by adaptation and partly by the simple persistence of chance variations fostered by the isolation and inbreeding, there has been no equivalent evolutionary divergence of the isolated groups of individuals of the parasite species. No adaptive changes have been necessary for it. It has indeed been broken into isolated groups of individuals, but no more than is normal to its life under conditions less novel. I have already pointed out the large variability that occurs within every Mallophagan species caused by the separation, more or less complete and persisting, of its individuals into little

groups and family strains each isolated on its host island or succession of self-reproducing islands.

But the change of plumage markings, or of bill shape or even of food and flight habit, of the separating host kinds splitting off from a common ancestor need mean nothing much for the parasite. So although in time we come to have, derived from a common ancestor, an American avocet and a European one, an American coot and a European one, we do *not* have an American avocet- or coot-parasite and a European avocet- or coot-parasite. But the parasite of the common avocet or coot ancestor of the two present bird species remains unchanged and is thus a single species common to the two geographically separated, specifically distinct, never-meeting, host species.

If this is a true explanation for the commonness of a parasite of two separated host species, it is likely also the explanation of the larger phenomenon of the general faithfulness of certain parasite species or genera to certain bird groups—families, or even orders. I do indeed believe that it is a commonness of the genealogy rather than a commonness of adaptation that is the chief explanation of this restriction of certain parasite groups to certain host groups. It is in my eyes an unusually clear example of the potency of heredity. There is more nature than nurture in the upbringing of the Mallophaga.

Isolation and inheritance, then, are the two evolution factors especially concerned in the species-forming and the distribution of the Mallophaga. Adaptation seems to play a very subordinate part. And this is a rather unusual condition in insect biology. The plasticity of insect nature combined with the stresses of insect life and the necessary shifts for a living, have resulted in producing among the insects some of the most striking examples of adaptive evolution to be found in the kingdom of life. In the face of this fact, this little group of parasites may have by the very exceptionality of its evolutionary behavior, an enhanced interest for us!

CASTRATION IN RELATION TO THE SECONDARY SEXUAL CHARACTERS OF BROWN LEGHORNS[1]

H. D. GOODALE

STATION FOR EXPERIMENTAL EVOLUTION

Introduction.—It has often been observed, in many sexually dimorphic species of birds, that a female occasionally occurs which exhibits many of the characters of her mate. Frequently associated with this condition are alterations, more or less pathological, in the ovary. It has been said also that the male sometimes, and in particular the unsexed male of the domestic fowl, presents characters resembling those of the female. However, it has been pointed out that the supposed resemblance to the female can also be interpreted as due to the failure of the development of the normal adult male characters. In other words, these modified males may be referred to either a juvenile or to a female condition.

These considerations led, then, to the following questions. Will removal of the ovary from the young female fowl cause her to assume the characters of the male? Will removal of the testes from the young male cause him to assume any female characters or will it cause him to retain his own juvenile characters or will it be without effect? For answers the Brown Leghorns seemed to furnish particularly favorable material, because: first, the adult plumage, which is strongly sexually dimorphic, is practically identical with that of the Jungle fowl; second, the comb of the female, while proportionally smaller than that of the male, is larger than that of the male of many other varieties; third, there are at least

[1] This paper with some changes was read before the American Society of Naturalists at Princeton, N. J., December 28, 1911. Since then the experimental results have been fully verified. Male characters have developed on 25 females, following ovariotomy. A complete account of the newer experiments will be published later.

three distinct stages in the development of the young bird's plumage before the adult color is reached. The first two stages do not exhibit sexual dimorphism, nor are they identical with that of the adult female. Sexual dimorphism appears first in the third juvenile plumage. At this stage, while the young female rather closely resembles the adult female, the young males in their *tout ensemble* are distinct from either the adult male or female, though sometimes feathers like those of the female may be found. A study of the characters of the Brown Leghorn capon or poullard, therefore, should show whether their characters are juvenile, male or female. For most characters, the results obtained from a preliminary set of experiments are clear cut.

Description of the Secondary Sexual Characters.—In Table I is given a comparative statement of the more pronounced secondary sexual characters common to nearly all races of domestic chickens. There are other differences between the sexes, which are more subtle and therefore not considered here. In Table II are given other secondary sexual characters found in the Brown Leghorns but not in all other races of chickens.

Comment on Tables.—Such exceptions to the general statements given in Table I as occur, are mainly negative, that is, they are characters which for one reason or another do not become patent, as for example, the failure of the whole or a part of the color pattern to become visible, particularly in the case of uniformly colored birds.

In considering plumage characters aside from shape of feather there are three features to be taken into account. First, the localization of color in certain definite regions of the body, thus forming the body pattern; second, the localization of color on definite regions of the feather, forming the feather pattern; third, the pigments themselves, which are associated with each pattern in various ways.

It is rather striking, that in spite of the numerous

TABLE I[2]

A COMPARATIVE STATEMENT OF THE CHIEF SECONDARY SEXUAL CHARACTERS OF DOMESTIC CHICKENS, COMMON TO NEARLY ALL VARIETIES

	Adult		Young of Both Sexes
	Male	Female	
Size, including comb	Relatively large.	Relatively small.	
Spurs	Well developed.	Absent.	
Plumage form	Hackle and saddle feathers long, narrow, pointed at tip.	Hackle feathers similar to those of male but relatively shorter and more rounded at tip; saddle feathers broad, relatively short and broadly rounded at tip.	Similar to female.
	Barbules absent on distal half of barbs of hackle, back, saddle, and wing bow feathers. Cf. Fig. 3, *A*.	Barbules absent from distal third of hackle feathers only; present elsewhere. Cf. Fig. 3, *D*.	Barbules present.
	Tail coverts, including sickles, long, curved and pointed.	Tail coverts, relatively short, broad and rounded at tips.	Similar to female.
Body color pattern	Numerous distinct color areas; viz., hackle, cape, back, saddle, wing front, wing bow, wing bay, wing bar, primaries, tail, breast and ventral surface.	Relatively few areas; viz., hackle, tail, primaries, (wing bay?), breast, ventral surface, and remainder of body.	Varies with different breeds.
Feather pattern	Usually uniform[3] or with central stripe.	Stippled or penciled when not like that of the male.	Varies with different breeds.
Behavior	Relatively erect carriage, pugnacious, frequently crows, rarely "sings," appears to lack brooding instinct.	Relatively horizontal carriage, not pugnacious, does not crow, but "sings" a great deal when in laying condition, has brooding instinct.	Peeps for a time, then follows a period when voice is rarely used until approaching maturity.

varieties of domestic chickens, there is, with one exception, only one basic *body* pattern, that of the Jungle fowl. (See table.) All other patterns, with the exception of the white crest of certain Polish, must be considered as modi-

[2] These tables make no pretense of giving all the characters which differ in the two sexes. I have also ignored minor details in some characterizations.

[3] Uniform, except as the under color can be distinguished from the surface color. See also text.

fications of the Jungle, usually by the loss or non-development of a part. I know of no other distinctive pattern in chickens, such as, for example, that exhibited by the Mallard in ducks.

TABLE II[2]

A COMPARATIVE STATEMENT OF THE CHIEF SECONDARY SEXUAL CHARACTERS OF BROWN LEGHORNS, OTHER THAN THOSE GIVEN IN TABLE I

	Adult		Juvenile (Third Stage)	
	Male	Female	Male	Female
Comb.....	Erect. Blade proportionately large.	Lops. Blade proportionately small.	Erect. Relatively large and of quick growth.	Erect. Relatively small and of slower growth.
Spurs.....	Present.	Usually absent, but frequently present in various conditions of development.		
Plumage color....	Hackle, reddish orange, with black central stripe; back and wing bow, dark crimson; saddle, reddish orange, often with black central stripe; wing bay, red; dorsal white area at base of tail; rest of body black.	Hackle, yellow, with dark-brown central stripe; breast, salmon; tail, primaries and concealed portions of secondaries, black; rest of body, dark and light brown, intermingled in pepper and salt fashion.	Mostly black, each feather being splashed with various amounts of red. Feathers of back often like those of young female. Body pattern of adult more or less clearly indicated.	Similar to adult but markings coarser.

The feather patterns fall into two groups, viz., those associated with sexual dimorphism and those not so associated. In the male there is no pattern of the first group. But penciling of the type found in the Dark Brahma female appears never to occur in the male and therefore belongs in the second class. Stippling is also usually distinctive of the adult female, but it occurs in the young male and under certain conditions (heterozygosis) in the adult male. In the Jungle female the stippling often approaches very closely the form of narrow concentric lines or vermiculations. Possibly the stippling of the Brown Leghorn female is due to the breaking up of such

vermiculations and so is not strictly comparable with that due to heterozygosis. However this may be, stippling is normally a female or a juvenile male character. The males corresponding to these two types of females usually have uniformly colored feathers ventrally. The dorsal regions are less constant in type, being usually uniformly colored or else striped. In other breeds the feather pattern may be alike in the two sexes.

The question of behavior depends upon so many conditions, that only a few of the numerous reactions have been mentioned in the table.

The following comments are intended to apply only to Brown Leghorns.

While the comb of the female usually lops to one side or the other, it does not always do so. There are indications, moreover, that by proper matings this character could be transferred to the male.

Spurs are usually absent from the female, yet they are occasionally well developed. Their presence can not be taken as a certain indication of the assumption of a male character by the female, for there was an old Scottish race in which both sexes were spurred. Nor need they indicate the presence of an abnormal ovary, for in one case in which they had become well developed at 9 months of age, the hen proved to be a splendid layer. These spurred hens are probably due to the presence or absence in the germ plasm of some definite determiner, as certain of my breeding experiments indicate.

The plumage color within certain limits is variable, so that it is a little difficult to describe briefly. American fanciers recognize only one type of plumage color for each sex, that described in the "American Standard of Perfection," but beside the "Standard" female there is one in which the salmon breast is replaced by one of nearly the same color as the back. Beside the "Standard" male is one in which the striping of the hackle and saddle feathers is lost, and third, one in which there is some red in the under parts. It is evident, moreover,

from experiments in cross breeding, that the body pattern of the Brown Leghorn is not a unit, but is composed of several parts.

These departures from the ideal and the probable variability in the gametic constitution of supposedly pure-bred stock may be expected to influence the behavior of the birds under castration. They indicate also that a character which at one time may behave as a secondary sexual character, at others forms a normal character of both races.

Experimental.—Without taking time to describe the details of the experiments, except to note that the gonads were removed from the chicks when they were 21–28 days old, that is, they were much younger than is the case in commercial caponization, we may proceed directly to a consideration of the results, taking up first the effects of castration on the male.

Seven of the castrated males reached four months of age, then three were accidentally killed. The autopsies on these three showed an entire absence of testicular material in two cases. The third had a tiny nodule, possibly testicular, on the mesentary near the former site of the testis.[4] All four survivors were kept until they were 16 months of age. Two were then killed for study. They developed the normal plumage of the male and were it not for the small comb and wattles they would have had nearly the same appearance as a normal cock (Fig. 1). They are, however, somewhat fuller plumaged and rather heavier looking birds than a normal cock. The spurs are well developed but on the other hand these capons are less active in their movements, are non-combatants and show no sexual instincts. They have never been heard crowing, though they may be made to squawk or even cluck like a *cock*.

One of these capons was somewhat anomalous in that he had much the same appearance as a normal cock. He had a large comb but did not crow. At one time he

[4] Unfortunately this material was not sectioned.

showed some inclination to pay attention to the hens, but as far as I was able to observe, it never went as far as an attempt at copulation. At the autopsy it was found that there had been an autoplastic transplantation of a bit of the testis.

FIG. 1. Brown Leghorn Capon. The colors are exactly those of the male as given in Table II.

It will have been observed from the foregoing description, that the small comb of these capons is the only character which might be considered female. In all other points the characters of the capon are the characters of the cock, sometimes exaggerated (feather length), sometimes infantile (crowing instinct). None are positively female, except perhaps the comb, which is much too large to be purely infantile, and too small and of the wrong proportions to be that of a normal adult female. On the whole it most closely resembles that of the *mature young female* before she has actually commenced to lay, or of the adult female when out of laying condition. Comb size is affected by so many conditions that the question as to whether or not the capon has a female type of comb is not easily answered, and therefore must await further studies.

We may turn now to the effects of castration on the

female. Unfortunately, only one of the females from which the ovary (naturally only the left, since it was assumed that the right had completely degenerated) was removed, reached maturity. There is no doubt as to the effect of ovariotomy on this individual (Fig. 2), which

FIG. 2. Female Brown Leghorn from which the ovary was removed. The colors, with the exception of some feathers as noted in the text, are those of the *male* as given in Table II. The long saddle feathers are hidden by the wing, but see Fig. 3, *C*.

commonly passed as a cock, with those unacquainted with the bird's history. Nevertheless, the assumption of male characters has not been quite complete, as is shown by a consideration of the following features. First, the presence of feathers on the back which are very much hen-like (Fig. 3, *B*). Second, the wing bow is poorly developed. Third, the shank is too short for that of a cock. In some points of behavior, such as lack of the crowing instinct, non-combativeness, cackle and general indifference to the hens, she is hen-like. On the other hand, her carriage is cock-like and by suitable means she has been made to cluck like a cock and even to pay a little attention to the hens, though this last reaction was produced only once or twice. The peculiar shape and carriage of the tail probably has nothing to do with the effects of castration, since this bird had only half a rump. Moreover, a rumpless cock occurred in this same strain.

Some additional light on the question is afforded by the effect produced by castration on a second female, which died at the age of four months. When the first feathers of the third stage began to appear, they were like those of the young male. The later feathers, however, were those of the normal female. The explanation of this anomalous behavior was found at the autopsy, for it showed the

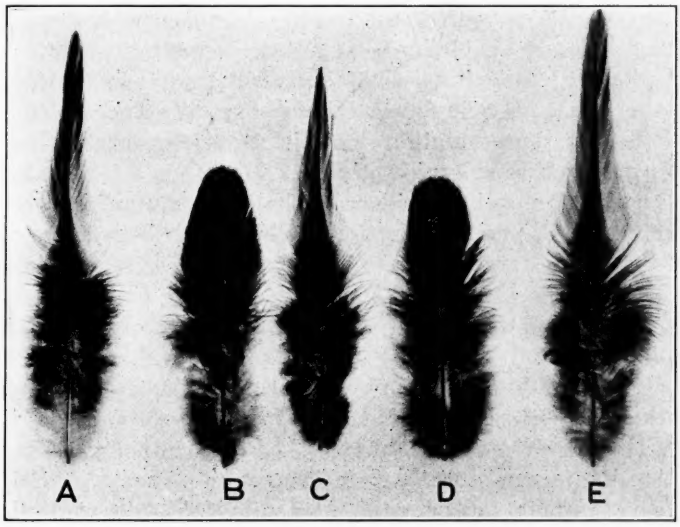

FIG. 3. Feathers from the saddle region of the various types of birds described. *A*, normal male; *B* and *C*, two sorts of feathers from the bird shown in Fig. 2; *D*, normal female; *E*, capon.

presence of an ovary about one half the size of that of a normal chick of the same age. As long as the ovary or its normal secretion was practically absent, the development of this female was along lines similar to that of the male, but with the regeneration of the ovary development returned to its usual course.

These experiments, then, indicate clearly that while the female may assume male characters following the removal of the ovary, the male assumes no positive female characters after removal of the testes.

Theoretical.—Certain of my breeding experiments have seemed to show that the Brown Leghorn plumage colors and pattern followed a sex-limited mode of descent. Certain difficulties, however, have arisen. As stated above, it has become evident that the coloration and pattern of the Brown Leghorns is not due to a single inheritable unit, but to a complex. This means that its more or less independent parts must be discovered and the mode of inheritance as well as the conditions under which each part becomes visible in the soma, worked out. Until this is done it will be impossible to say what part sex-limited inheritance plays in determining sexual differences. The following representation, then, is merely an attempt to formulate a working hypothesis.

The male may be considered to be duplex for an internal secretion *S*, produced by the testes, which is necessary for the full development of the comb and less clearly for the crowing instinct and sexual behavior, but not for plumage and spurs. In the female this secretion is replaced by one *S′* produced by the ovary. (*S′* may, perhaps, stand in some simple chemical relation to *S*.) To its effect is to be referred the female's form and color. When the ovary is removed or becomes pathological so that its normal secretion is no longer produced, then the male characters develop to an extent which is determined by factors at present unknown to us. Nor are we concerned here as to what part of the ovary or testis produces this secretion (or secretions, for *S* and *S′*, respectively may well represent a number of secretions which behave in the same general way). In any case the internal secretion may be conceived to be associated with sex in the same manner as any other sex-limited character. The formula for the male would then be $S♂\ S♂$, that for the female $S♂S′♀$. *S′* is of course to be considered dominant to *S*. If this scheme represents the actual condition of affairs it may not be necessary to suppose that the female Brown Leghorn is simplex for *L* where *L* represents the whole or a part of the male Leghorn

pattern complex, for S' might be able to transform two doses of L into the condition observed in the female as well as one dose. This is, however, a matter to be tested by experiment.

In insects, Meisenheimer and others have shown that castration is without effect on the secondary sexual characters of either sex. This lack of association between the secondary sexual characters and the gonads may find its explanation in the absence of a modifying secretion from these forms, the secondary sexual characters being determined solely by differences in the gametic constitution of the sexes, for example of the form AA in one sex and AB in the other, B being dominant over A and linked with the sex determiner, in the usual fashion for a sex-limited factor.[5] Secondary sexual characters of insects would then belong to a different category from those of the birds. There is some evidence, however, that certain characters of the female fowl are not under the control of the secretion of the ovary, for they do not become male-like after the removal of the ovary and therefore are like the insects in this respect. This point requires further study.

There is one more point to be considered. I have shown that in the Brown Leghorns as well as in Rouen ducks that the male does not assume female characters as a result of castration. Does the adult male of other sorts of birds ever exhibit female characters? An affirmative answer is possible only in those cases in which the juvenile plumage of the male is like that of the female. But if we consider only those cases in which the juvenile male plumage is unlike that of the female, we shall find that conclusive evidence on this point is wanting, at least I have thus far been unable to secure such evidence.

[5] There are, of course, other ways of representing this association.

SIMPLIFICATION OF MENDELIAN FORMULÆ

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PROFESSOR BESSEY in his recent presidential address[1] expresses the opinion that Mendelian terminology is needlessly complicated. This opinion most biologists will heartily endorse, and not a few Mendelians will be among their number. For those who work most extensively with Mendelian formulæ feel most keenly the need of simplification in these the tools of their investigations.

Professor Morgan, in the January NATURALIST,[2] makes a commendable effort to introduce reforms. I desire heartily to endorse his effort, but would suggest certain modifications in method.

The Mendelian may say in justification of existing usage that it has arisen naturally step by step as knowledge of Mendelian phenomena has advanced, but this is of course no justification of its continued use, if it has become a hindrance rather than a help in the further advance of knowledge.

Morgan clearly points out the two historical steps by which present usage was reached. The first of these was Mendel's original recognition of segregating dominant and recessive characters existing in contrasted pairs, and his convenient designation of the former by capitals and of the latter by small letters. This usage answered perfectly so long as only a single modification of any character came under consideration, and indeed Mendel's observations did not go beyond this. But this system broke down when characters more complex in nature came under observation, as for example when Cuénot showed that more than a single differential factor exists between gray mice and albino mice. (2) The ingenious and useful

[1] *Science*, January 3, 1913.

[2] Vol. 47, pp. 5–16.

"presence and absence" hypothesis of Bateson was the second step which led to our present usage. On this hypotheses gray in mice is not the allelomorph of white, but of *no-gray;* while the allelomorph of white is color, or more properly speaking white is equivalent to *no-color* and *this* is the allelomorph of color.

Both of these steps have been amply justified by their utility in making possible the prediction of the previously unpredictable consequences of particular crosses.

It was natural that in applying the presence and absence hypothesis the usage of Mendel should have been retained, in accordance with which capital letters were used as the symbols of dominant characters and small letters as the symbols of recessive characters. But this retention has involved most unfortunate consequences and is, I believe, the real seat of our present difficulty.

Mendel's small letters stood for realities as truly as did the capitals. His *A* was a round form of pea, his *a* was a wrinkled form of pea; his *B* was a yellow-seeded, his *b* a green-seeded pea. But the significance of these terms has been changed under the presence and absence hypothesis. *A* still means a round pea, but *a* is simply a *not-round* pea; it may or may not be wrinkled. Likewise *B* is still a yellow-seeded pea, but *b* is nothing but a *not-yellow* pea; it may or may not be green under the presence and absence hypothesis. For all that *b* signifies now, the pea may be blue, violet, indigo or carmine.

It is most unfortunate, therefore, that the small letters, having lost their original significance, were not discarded altogether, for under the presence and absence hypothesis they have done nothing but cause mischief.

The investigator who employs them starts out well intentioned with a clear notion that the small letters stand for negation only, that they are merely signboards to show what characters he is talking about, but presently, unless he is unusually careful, we find him talking about them as if they stood for *something,* instead of nothing; he speaks of repulsions and couplings or associations

between *a* and *B*, or even between *a* and *b*. Think of it! How can *something* be coupled with *nothing?* How can *nothing* be inseparably bound up with *nothing?* It seems to me the consequent effect on inheritance is *absolutely "nothing"!*

Not only do the small letters thus lead to confusion of thought, they also tend to make formulæ needlessly cumbersome, for they call for the use of *two* symbols for every character difference dealt with. These two symbols also are so much alike that both printer and reader are in momentary danger of confusing them, with the consequence that what is *is not,* and what is not *is!*

The small letters are not indispensable to accurate and exhaustive analysis of Mendelian phenomena, or to lucid exposition of them. See, for example, the fundamental researches of Cuénot into the color inheritance of mice, and his classic "notes" describing them. Like Cuénot, I have not found the use of the small letters necessary; but among nearly all other Mendelians the double terminology has become so nearly universal that a different usage seems almost to demand an apology. Indeed Lang[3] has suggested that such offenders against uniformity as Cuénot and I should be haled before an International Congress and be *directed* to conform; since which time I had almost abandoned hope of ever seeing improvement in the current confusing system, but Morgan's protest and proposal gives me new courage.

What we need first of all to symplify our present usage is to *abandon the dual terminology.* Where we are dealing with a *single* set of variations, let a *single* set of symbols suffice. Let us give up either the small letters or the large ones, it matters not which. If we retain *A*, then we have no need of *a*, for it is not, as Morgan at one time seems to assert and at another to deny, the "residuum" when *A* is lost; it means on the presence and absence hypothesis nothing but this, that *A* is not present. The rest of the organism is the "residuum." Morgan points

[3] *Zeitsch. f. ind. Abstammungs- und Vererbungslehre,* 4, p. 40, 1910.

out and his paper illustrates amply how under the dual system "the letters used may unintentionally come to stand for different things." The obvious thing to do, if we attempt reform, is to omit the superfluous symbol, either the small letter or the large one.

Morgan, however, clings to the dual nomenclature, but suggests a reversal of the usual significance. Thus the factor for pink-eye, he assumes, is present only in animals which are *not* pink-eyed, and the factor for black body color, he suggests, is present in all sorts of flies *except* those which are black bodied. This is confusion worse confounded.

But, seriously, I do not see that it is possible to improve the existing terminology, so long as we use two terms of opposite significance with reference to a single germinal variation. Certainly merely reversing the significance of existing terms will not do it. What we need first of all is *one set of symbols,* used in a single significance.

If this reduction is allowed, then I think that another aspect of Morgan's proposition might be extremely useful, viz., *that a mutation which behaves as a recessive in crosses be designated by a small letter.* This proposition was put into effect more than three years ago in a paper dealing with color inheritance in mice, though Morgan does not seem to have observed it. See Castle and Little (1909).[4] In the paper cited, three recessive color factors of mice were designated by small letters, viz., "*d*, the dilution factor"; "*s*, the factor which causes *spotting* with white;" and "*p*, the pink-eye (or paucity) factor."

In that same paper all *dominant* color factors of mice were designated by capitals. This seems to me a very necessary complement to the use of small letters to express recessive variations, and is in entire harmony with Mendel's original usage. But neither of these proposals can help matters much, *unless we discard the duplicate set of symbols, which is the chief cause of present confusion.* Thus if we use *s* for spotting, then we have no

[4] *Science,* N. S., Vol. 30, pp. 312–314.

occasion to use *S* for no-spotting. We simply leave out all reference to spotting, and we shall understand that there is none, but that the normal condition prevails.

To be very explicit, my proposals for simplification of Mendelian terminology are three:

1. To abolish the current dual terminology and use only *one symbol,* where a single variation from the normal is involved.

2. To use a *small letter* to designate the factor responsible for a variation which is *recessive* in crosses with the normal.

3. To use a *capital letter* to designate the factor responsible for a variation which is *dominant* in crosses with the normal.

These proposals were made in substance in publications of the year 1909 and are here renewed under encouragement of Morgan's suggestive paper. Let us see how they would work if applied to the cases enumerated by Morgan. The eye color series described by Morgan, *l. c.,* page 13, involving three recessive mutations, is as follows:

	Revised Terminology	Morgan's Terminology
Red	*normal*	*PVE*
Vermilion	*v*	*PvE*
Pink	*p*	*pVE*
Pink-vermilion	*pv*	*pvE*
Eosin	*e*	*PVe*
Vermilion-eosin	*ve*	*Pve*
Pink-eosin	*pe*	*pVe*
Pink-vermilion-eosin	*pve*	*pve*

The revised terminology is obviously shorter and simpler. It is obtained by merely omitting the capital letters from Morgan's terminology, letters which stand only for negations. The symbols used are suggestive of the names employed for the various color categories of eyes, whereas in Morgan's terminology the most conspicuous symbols are suggestive only of other categories than the true one.

The revised terminology is more convenient than

Morgan's in calculating the expected result of any mating, and it is equally reliable. The result of every possible mating within the series can be readily computed without the confusing presence of the large letters.

To those who have grown accustomed to the presence and absence terminology the objection will suggest itself that in naming the recessive character and ignoring its allelomorph, we are naming an absence or negative and disregarding what is present and positive. But this does not follow. Because a character is recessive it does not follow that it is negative. I quite agree with Morgan that the physiological condition which produces an eosin eye is as real as that which produces a vermilion, a pink or a red eye, and no mere negation; it is simply different. It is quite impossible to decide, from its behavior as a dominant or recessive in crosses, whether a character is positive or negative. This I have pointed out elsewhere (1911) and the same view has been repeatedly expressed by Shull. We have on record many instances in which one and the same character may behave at one time as a dominant, at another time as a recessive.

Our terminology may well recognize the dominant or recessive behavior of a variation, without implying anything as to its positive or negative nature, which must in many cases be conjectural or possibly non-existent. Different gradations of color, such as we have in the eye-series of Drosophila described by Morgan, may result merely from quantitative variations in cell constituents and consequent activities, nothing being lost. This idea concerning the possible nature of Mendelian factors in general I have developed elsewhere, concluding that "it is the substantial integrity of a quantitative variation from cell-generation to cell-generation that constitutes the basis of Mendelism. All else is imaginary."[5]

Morgan applies his altered system of nomenclature also to the body-color series and wing mutation series which he has discovered. This nomenclature we may simplify,

[5] AMERICAN NATURALIST, Vol. 46, p. 358, June, 1912.

as we did in the case of the eye-color series, without impairing its utility.

BODY-COLOR SERIES

	Revised Terminology	Morgan's Terminology
Wild fly	*normal*	*YBES*[6]
Yellow	*y*	*yBES*
Yellow-black	*yb*	*ybES*
Ebony	*e*	*YBeS*
Sable	*s*	*YBEs*[7]

WING-MUTATION SERIES

	Revised Terminology	Morgan's Terminology
Wild fly	*normal*	*MR*
Miniature	*m*	*mR*
Rudimentary	*r*	*Mr*
Rudimentary-miniature	*mr*	*mr*

The taste of the reader will govern his choice between these two systems. Doubtless either can be used successfully, though the revised terminology seems to me preferable on the ground of simplicity and suggestiveness.

In the series with which Morgan has dealt, all the mutations under consideration are *recessive* in character, so that one can read the names of the varieties directly from his formulæ, if one disregards altogether his large letters and pays attention only to the small ones. To insure this I have suggested omitting the large ones.

But if one were to extend Morgan's terminology to a series in which *dominant* mutations as well as recessive ones occur, hopeless confusion would result. For here some of the large letters would stand for mutations, while others would stand for the negation of mutations, so that without a key constantly at hand the formulæ would be unusable.

If, however, we use the *single* system of symbols as I have suggested, a series which includes both dominant and recessive mutations may be handled without confusion. In this case every symbol is significant, and its

[6] For simplicity I here use *E* instead of Morgan's *Eb*.

[7] Morgan's list here contains *S*, but this I suspect is a misprint for *s*; if so, it is a living witness to the dangers of the dual system.

dominant or recessive character is indicated by the symbol, whether large or small. For example, consider the mouse-color series as described by Castle and Little (1909). In the paper cited, nine color factors were described, three of which clearly recessive have already been mentioned, viz., *d*, *p* and *s*. The remaining six were considered dominant factors. Mr. Little has since suggested, and I think with good reason, that one of them had better be omitted, since its existence has not been demonstrated beyond question. The six as given were *C*, the color factor; *Y*, the yellow factor; *Br*, the brown factor; *B*, the black factor; *R*, the restriction factor (producing a yellow coat); and *A*, the agouti or gray factor.

Mr. Little would omit either *C* or *Y*, since it has not been shown beyond question that the effects which had previously been ascribed to these two are not due to one and the same agency.

With the eight symbols which would remain, three being small letters, the others being or beginning with capitals, it is possible to write, without duplication of terms, formulæ descriptive of the entire color series. But in so doing it would be necessary to designate the original or wild form in terms of factors supposed to be lost in its derivatives, and which have only come to light through such loss. This, as Morgan points out, involves redescribing the wild form every time a mutation arises and should be avoided if possible. I therefore favor Morgan's suggestion that each mutation as it arises be given some suitable descriptive name, the initial or other significant letter of which shall be its symbol. If, as is commonly true, the mutation is recessive in crosses with the wild or original type, its symbol will be a small letter. But if the mutation is dominant,[8] its symbol should be a large letter.

The original or wild type *need not be described in terms of its mutations,* as every duplicate system of terminology, even Morgan's, requires. The system would ac-

[8] I have met two dominant mutations in guinea-pigs, one in rabbits, and one in mice, so that they can scarcely be called rare.

cordingly be capable of indefinite expansion without constant remodeling.

I favor Morgan's further suggestion that as new forms arise through recombination of simple "mutations" these be described, so far as possible, in terms of the simple mutations composing them. This principle is clearly illustrated in the names chosen by Morgan for the eye color series of Drosophila. It is surprising how little change this system necessitates in the common names with which we are already familiar, for example, in the mouse-color series.

The color mutations[9] of mice with which I am personally familiar number seven. If all of these are independent, *i. e.*, not "coupled" or "associated," there should be theoretically possible 127 different combinations involving one or more of them. A considerable proportion of these combinations has been produced in my laboratory in the course of the last twelve years, the earlier and simpler ones by Dr. G. M. Allen or myself, the later and more complex ones by Mr. Little, who has in press an extensive paper dealing with his investigations. I shall deal with the series as known up to 1909. The historical order of appearance of the mutations is now unknown; I shall place them in the alphabetical order of the symbols used. It is also unknown whether each of them arose directly from the wild type. More probably they did not, but experiment shows that they might have done so, since each behaves in crosses as if it had a distinct and independent basis in the germ-plasm.

WILD TYPE AND ITS SEVEN MUTATIONS

1. *Wild* = gray.
2. *a* = albino (transmitting gray in crosses).
3. *b* = black.
4. *c* = cinnamon.
5. *d* = dilute.

[9] I use the term mutation in the sense of unit-factor variation, not in that of DeVries.

6. *p* = pink-eyed.
7. *s* = spotted.
8. *Y* = yellow.

The *a* mutation, however combined, if present in a homozygous condition, prevents the development of pigment in the skin, hair or eyes. The *d* mutation, under like circumstances, makes the pigmentation of the coat dilute, or pale; the *p* mutation reduces even more strongly the pigmentation of coat and eyes alike, but does it in a different way; the *s* mutation causes pigment to be altogether wanting in certain areas of the coat more or less definite in position and extent, which areas accordingly appear as white spots.

Combinations of these four mutations present no difficulties of description or recognition, though breeding tests alone suffice to differentiate the several sorts of albinos, since all look alike. The nomenclature also is perfectly simple. Thus,

ap = albino transmitting the pink-eye mutation in crosses.

adp = albino transmitting both dilution and pink-eye in crosses, etc.

Combinations of *b*, *c*, and *Y*, one with another, form the fundamental and best known color varieties, which will now be considered.

In the *b* mutation, the fur is black; in the *c* mutation, it is brownish gray, called cinnamon. In the *Y* mutation, the coat is yellow. Of the several mutations mentioned, *Y* alone is dominant over the wild gray, but it occurs only in a heterozygous state, and hence never breeds true.

The complete color series involving these three mutations, but excluding all others, is as follows:

Wild = gray.
b = black.
c = cinnamon.
bc = black-cinnamon (chocolate).
Y = yellow (giving also gray offspring).
bY = black-yellow (giving also black offspring).

cY = cinnamon-yellow (giving also cinnamon offspring).
bcy = black-cinnamon-yellow (giving also black-cinnamon offspring).

To express the modification which this series undergoes if the *d* mutation is added to it, we need only prefix the symbol *d* to each of the formulæ given and omit the term *wild* as no longer applicable. The series then becomes

d = dilute gray.
db = dilute black.
dc = dilute cinnamon.
etc.

Similarly an added *p* factor gives us the series

p = pink-eyed gray.
pb = pink-eyed black.
pc = pink-eyed cinnamon.
etc.

Also an added *s* gives us the series

s = spotted gray.
sb = spotted black.
sc = spotted cinnamon.
etc.

Adding both *d* and *p* gives us the series

dp = dilute pink-eyed gray.
dpb = dilute pink-eyed black.
dpc = dilute pink-eyed cinnamon.
etc.

Adding *d* and *s* gives us the series

ds = dilute spotted gray.
dsb = dilute spotted black.
dsc = dilute spotted cinnamon.
etc.

Adding *p* and *s* gives us the series

ps = pink-eyed spotted gray.
psb = pink-eyed spotted black.
psc = pink-eyed spotted cinnamon.
etc.

Adding simultaneously *d*, *p* and *s*, gives us the series

dps = dilute pink-eyed spotted gray.
dpsb = dilute pink-eyed spotted black.
dpsc = dilute pink-eyed spotted cinnamon.
etc.

We thus secure eight different variations of the fundamental color series, or a total of sixty-four colored varieties. By prefixing *a* to the formula for each of these varieties, we obtain formulæ for sixty-four different types of albinos, which though all looking alike (being snow white), yet would transmit in crosses the characteristics each of a different one of the sixty-four colored varieties.

We have thus accounted for the entire one hundred and twenty-eight variations which theoretically should result from recombining seven distinct mutations with the original form from which they sprang, and this has been done in relatively simple terms. Only one formula in the whole 128 contains as many as seven letters. *This is adpsbcY,* and would be read "an albino transmitting dilute pink-eyed spotted chocolate and dilute pink-eyed spotted yellow." All the other formulæ would contain from one to six letters. The current presence and absence system would require *sixteen letters* in every one of the 128 formulæ to express the same facts, and the same letter would in some of the formulæ be a capital and in others a small letter, so that the constant close attention of the reader would be required to decide in each case whether a particular mutation was or was not present. Morgan's system would be only slightly less cumbersome for it would require in each formula fourteen instead of sixteen letters, and the same confusion would result from the presence of duplicate large and small letters. The mere statement of these facts is sufficient to show that Mendelians can easily simplify their formulæ and make themselves more readily intelligible to each other and to their fellow biologists, if they are only willing to do so.

There is another reason why I favor Morgan's terminology (as here simplified); it commits us to no physiological theory, but simply states facts. We are not

required to suppose that the wild form contains a number of factors which by mutation have been lost. We may still do so, but we are not *forced* to do so. We are free to suppose with Morgan that merely a "readjustment" has taken place, and to make no assumption as to its nature, unless we choose to do so. This course does not prejudice the investigator of the physiology of color production but leaves him free to frame such hypotheses as will from his point of view best meet the situation. He is not bound down, for example, to a hypothesis of chromogen and ferments and so tempted with Riddle to throw over all Mendelism simply because Mendelians have in his opinion misinterpreted chemical facts.

That terminology evidently is most desirable which states demonstrated facts most clearly and simply, and makes fewest assumptions as to their explanation. Otherwise the investigator may be led to conclusions based on his terminology rather than his facts, and this can lead only to disaster.

NOTES AND LITERATURE

SOME RECENT ADVANCES IN VERTEBRATE PALEONTOLOGY

THE study of the extinct life of the globe must ever be the central and basal point for an understanding of the manner in which evolution has taken place. The ultimate appeal in the theory of descent must necessarily rest with the facts in the history of animal and plant life as it is read from the records in the rocks. Organic evolution is now so firmly established in the minds of present-day scientists that a statement of its truth is no longer needed. But it is well for us to be cautious in our statements about evolution, in not expressing more than we can prove. It is quite possible that the vertebrates come from the arachnoids as Patten contends, but the evidence on this point is wholly lacking. It is also possible, nay even probable, that the crossopterygian ganoids gave rise to the land vertebrates and even a single species of this group *may* have been such an ancestor, but no one knows whether they did or not and to state, as many of our recent zoological text-books have done, that such *was* the origin of land vertebrates, is to state what is not known. It is true that the Stegocephali may have given rise to the reptiles, indeed there is very little difference between some of the reptiles and some of the Stegocephali but the proof of the descent of all reptiles from any one or all of the groups of the Amphibia is more than any one has yet given. The birds may and possibly did arise from the reptiles but the early stages are still unknown. It is the firm belief of many that paleontological proof will be forthcoming for sustaining the ideas expressed by the theory of organic evolution but the facts as they are brought to light by the study of paleontologists do not serve to show that this is true. Smith Woodward says that connecting links or even approximate links between nearly all of the great vertebrate groups are still wanting from our large collections. It may safely be said that 99 per cent. of all the collections of fossil vertebrates in the world serve to show diversifications of various groups of animals and *not* to connect them in any satisfactory way. There are, to be sure, connections and

definite ones between the smaller groups of many vertebrates but not between the larger ones. Many writers, especially writers of text-books, assume much more than they can prove, and the great majority of the modern zoological text-books are sadly behind the times in matters of paleontological knowledge and works that serve as standards and bases for the construction of more elementary texts make the most bald misstatement of facts.

The general trend of paleontological research is to round out our knowledge of the diversity and structure of many groups; the establishment of a few new groups especially of lower rank; no one save Jaekel having had the temerity to propose new groups higher than sub-classes.

Not all of the recent work in vertebrate paleontology is reviewed here. Many excellent works have been sufficiently noted elsewhere but sufficient is here given to show the tendency of thought and work among the vertebrate paleontologists; that of attention to matters of structure, occurrence, association, interpretation of matters of organization and relationship, all of which are fundamental to safe conclusions regarding the larger problems of phylogeny. It is perhaps too early to arrive at such conclusions in regard to phylogeny as we should wish to have—but paleontology is 100 years old and more!

One of the more recent publications from the press of Gustav Fischer is a volume entitled "Die Abstammungslehre," a collection of twelve essays on the descent theory in the light of recent researches. The ninth essay is one by Dr. O. Abel, in which he discusses "Die Bedeutung der fossilen Wirbelthiere für die Abstammungslehre." Dr. Abel says there were two ways in which he might discuss his subject, either by giving a short résumé of the investigations of paleontologists or by discussing the methods of paleontological investigation and the bearing of the results of these methods on the descent theory. He has chosen the latter and has discussed his subject in a masterly manner. He has divided his paper into three parts with various sub-headings and discusses a phase of paleontological methods in each division. He discusses the alleged lack of material among paleontological specimens and shows that, in a few instances at least, there is more material available for study of the forms than there is for many of the recent species. The discussion of the value of reconstructions in paleontology

is illustrated by various reconstructions of the pterodactyls from Wagler's restoration of *Pterodactylus* in 1830 to Eaton's restoration of *Pteranodon* in 1910. Dr. Abel contends that the reconstruction of a fossil species is valuable, since it gives graphically all that is known of that form at the time the restoration is given. The fact that it may be wrong is no reason why restorations should be abandoned, since they record the progress of our knowledge of animal forms.

Dr. Abel uses as an illustration of the genetic line of descent that of the Cetacea, in which group he is an acknowledged authority. His discussion is illustrated from previous papers. The descent of the whales has been brought about in the reduction of certain structures, such as the teeth and the limbs. As an illustration of a line of descent which has operated in the way of complication of structures he cites the elephant series which has been made well known through the researches of Andrews and Osborn. The reader notes with a sigh of relief that but little attention is given to the line of descent of the horse ("das Paradepferd der Paleontologie").

Dr. Abel's selection of the sea turtles as an example of Dollo's law that "A structure once lost or reduced in development of a race is never regained" is timely and refreshing since it has been but little used. He gives Wieland's restorations of *Archelon* and bases his conclusions on Dollo's researches on the phylogeny of *Dermochelys coriacea.* He discusses, in the two last sections of the chapter, "Stufenreihen" and illustrates his discussion by Dollo's work on the dipnoan fishes, illustrating forms from the lower Devonian to recent and, in the last section, "Ahnenreihen" he discusses the derivation of the *Sirenia* and illustrates by the pelvic girdles of the sea cows from the middle Eocene to recent.

The concluding remarks show a strong desire to further the relation between paleontology and zoology "damit wir mit vereinten Kräften unserem gemeinsamen Ziele, der Aufhellung der Stammesgeschichte, entgegenschreiten." In view of the fact that paleontology has been largely in the hands of the geologists this is a relation much to be wished.

Charles W. Gilmore[1] has described an interesting new form of Alligatoridæ from the "Hell Creek Beds" (Upper Cretaceous) of Montana. Only a portion of the skull was preserved for description. This has been restored into the shape of the

[1] *Proc. U. S. Natl. Museum,* 41, 297–302, 2 pls.

modern *Alligator* skull. After comparison with *Diplocynodon*, *Alligator* and *Bottosaurus*, all members of the Alligatoridae, Gilmore has described the new alligator as *Brachychampsa montana*, new genus and species. He gives as the fundamental generic character of the form

> In the absence of a roof-like covering formed by the premaxillaries over the anterior part of the external nares, *Brachychampsa* differs from all known alligators, both recent and extinct.

Some of us may be inclined to question the validity of this character for a genus but further study will doubtless establish the form on a safe basis.

Dr. W. D. Matthew has reviewed briefly[2] the ideas relative to the posture and habits of life of the great ground sloth, *Megatherium*, and its allies from the Pleistocene of North and South America. Under Dr. Matthew's direction there has been prepared a small group of four of these large brutes in the attitudes which have been suggested as possible by the study of their skeletal anatomy. Two genera are represented—*Lestodon* and *Mylodon*. The *Lestodon* skeleton is mounted in the familiar pose of the *Megatherium* reared against a tree trunk and one *Mylodon* is digging at the roots of the same tree. The writer says:

> These poses illustrate the theory of the habits of the ground sloth deduced by Owen from the study of the skeleton—a model of scientific reasoning whose accuracy has never been impugned.

The same writer in a short article[3] describes a recently mounted skeleton of *Agriochœrus* as "a tree-climbing ruminant." The history of this genus is interesting in that

> its various parts have been referred to no less than three mammalian orders, the head to the artiodactyls, the fore foot to the creodonts and the hind foot to the Ancylopoda.

Dr. Matthew opens his paper with the remark that

> It seems somewhat paradoxical to imagine a ruminant climbing trees.

He says further:

> The *Agriochœrus*, however, while a member of the Oreodont family, and like them provided with ruminating teeth, had the limbs and feet modified in such a way as to enable it to climb trees as readily as a jaguar or other large cat.

[2] *American Museum Journal*, XI, No. 4, p. 113.
[3] *American Museum Journal*, XI, No. 5, pp. 162–163.

No one is more entitled to a view on this subject than Dr. Matthew and even if we find it hard to accept his view of such a paradox yet it behooves us not to be too skeptical.

Dr. Bashford Dean[4] has described a new "fossil aquarium" recently installed in the American Museum of Natural History. Under his direction has been executed a group of Devonian fishes,

> all from a single locality (Cromarty) and a single rock layer in the Old Red Sandstone of Scotland, with the best evidences therefore, that the creatures shown really existed side by side.

The fishes shown seem to be swimming through the water as if alive. It must be a very attractive group to museum visitors.

A very interesting and extremely useful work on ichthyosaurs and plesiosaurs has been issued (1910) from the British Museum (Natural History) as "A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay," Part I, compiled by Dr. Charles W. Andrews. The catalogue is largely based on the Leeds Collection which the British Museum has been acquiring for the past twenty years. The volume is issued in the usual excellent form of all the previous British Museum catalogues, the illustrative work being photogravure, zinc line and lithograph, all executed with great care and attention to details.

The frontispiece is a photogravure of a nearly complete, mounted skeleton of a plesiosaur (*Cryptocleidus oxoniensis*), a dorsal view of which species has been used by Abel for the frontispiece to his "Paleobiologie." The introduction discusses the taxonomic characters of the ichthyosaurs and plesiosaurs, the fauna of the Oxford clay and the distribution of the vertebrates. A single species of *Opthalmosaurus* is discussed, and the details of its anatomy are contained in the first 76 pages of the work, illustrated by 42 text figures (including a restoration of the skeleton) and two lithographic plates. Aside from a discussion of the possible identity of *Opthalmosaurus* and *Baptanodon* of America, the writer has confined his remarks to the osteologic details.

The plesiosaurs are more abundantly represented in species than are the ichthyosaurs. There are four genera discussed in the last 120 pages of the volume, illustrated by 52 text-figures, 8 lithographic and one photogravure plate (containing three restorations of the various forms). As in the previous portion

[4] *Amer. Mus. Journal*, XI, No. 5, p. 161.

the writer has confined himself to the discussion of the details of osteology and this will make the work doubly useful to students who will find here an unbiased statement of the facts of structure of these two interesting groups of vertebrates. The work will thus be regarded as a standard book of reference on the forms there discussed. It may be regretted by some that the author has neglected the excellent opportunity to discuss such interesting factors as hyperphalangy, hyperdactyly, phylogeny, reduction of structures due to aquatic life, but perhaps this would be out of place in a museum catalogue and we may hope to have the views of Dr. Andrews on these subjects at some other time. The second volume of the series proposes to deal with the crocodiles and pliosaurs of the Oxford clay. The work will be looked for with much interest.

In a recent paper on *Edestus*[5] Dr. O. P. Hay discusses a recently acquired specimen of this interesting Carboniferous shark from the Des Moines Stage of Iowa, discovered in a coal mine near Lehigh some 18 years ago by a miner. The specimen shows the interesting relation of the so-called *spines* which have been assigned various places by various writers. The specimen seems to leave no doubt that the objects regarded hitherto as *spines* are in reality the mandibular and maxillary cartilages of a peculiar shark. Portions of the nasal and post-nasal cartilages are preserved and Dr. Hay indicates a depression as the olfactory pit. The cartilages are so crushed that the nature of the orbital cavities can not be determined. The maxillary cartilage is somewhat larger than the mandibular, as in the modern sharks. The paper is a very interesting contribution to the subject of Paleozoic sharks. He suggests that the forms *Toxoprion, Helicoprion* and *Lissoprion,* at present known only from detached pieces, may in time prove to have the relations exhibited by the present new species of *Edestus;* a relation which Dr. Eastman has claimed for some time obtained in the forms.

A new mosasaur is indicated by Charles W. Gilmore[6] based on imperfect remains from the Cretaceous of Alabama. Mr. Gilmore is inclined to establish a new genus on the characteristic form of the teeth of the new form. He calls the new genus *Globidens,* deriving his name from the Latin *globus* and *dens,* contrary to the usual custom of employing Greek roots for generic

[5] *Proc. U. S. Natl. Museum,* 42, 31–38, pls. 1–2, April 25, 1912.

[6] *Proc. U. S. National Museum,* 41, 479–484, pls. 39–40, January 31, 1912.

terms. The species is without doubt valid and is a very interesting one in showing a new type of tooth for the mosasaurs, wherein the tooth is a rounded ball instead of being sharp as in the majority of known mosasaurs. From its rarity one may be inclined to question the normal condition of the teeth, but all the teeth display the same characters, so Mr. Gilmore is justified in his assumptions of the distinction of the form so far as the evidence goes. The species is said to be related to *Platecarpus* which is the common mosasaur of Kansas; but we may question whether it is a true mosasauroid.

Mr. Maurice G. Mehl[7] has described and illustrated an incomplete skull of the interesting and little known cotylosaur, *Pantylus cordatus* Cope, from the Permian Red Beds of Texas. The species has been given the rank of a suborder, the Pantylosauria, by Case in his monograph of the Cotylosauria. The form is, however, known only from the skull and such reference may be subject to revision. Mr. Mehl was able, from the recently acquired material, to more fully describe the dentition of this mollusc-feeding animal. He illustrates his discussion by several line figures.

The history of the dinosaurs will always be an interesting topic for paleontologists. The recent contribution by Mr. Charles W. Gilmore[8] is an attempt toward the completion of the history of this group of animals, wherein he describes "The Mounted Skeletons of *Camptosaurus* in the United States National Museum." His discussion is illustrated by drawings and photographs with a map of one of the Como, Wyoming, quarries showing the positions of the *Camptosaurus* bones in the quarry. The skeletons of the two species are mounted in the attitudes of walking on all fours and the erect attitude, which was possibly characteristic of many of the Theropoda. The animals are represented as being semiplantigrade in the hind foot and semidigitigrade in the fore.

Walter Granger[9] has given a few notes on the locality and manner of collection of "a new specimen of the four-toed horse" discovered "in the extreme northwestern corner of Wyoming, in the Wahsatch formation of the Big Horn Basin." Since the form had previously been known only from fragments of jaws containing teeth, the recent find is a remarkably large addition

[7] *Journal of Geology*, XX, No. 1, 21, 1912.
[8] *Proc. U. S. Natl. Museum*, 41, 687–696, pls. 55–61, February 8, 1912.
[9] *American Museum Journal*, XI, No. 3, pp. 85–88.

to the already rich collections of the American Museum. It is to be hoped that the skeleton will be shortly described.

"A Revision of the Amphibia and Pisces of the Permian of North America with a Description of Permian Insects" is the work of E. C. Case, Louis Hussakof and E. H. Sellards, issued as Publication No. 146 of the Carnegie Institution of Washington, on December 20, 1911. The larger part of the work, 148 pages, 51 text-figures and 25 plates, is given to the discussion of the Amphibia which constitutes Dr. Case's contribution to the volume. Ten families of Amphibia are discussed in an historical, systematic and morphological manner, the last two being given approximately equal space. The "historical" portion of the discussion consists of the history of discovery and the taxonomy of the Permian forms as viewed by various writers from Cope (1875) to Broom (1910). The chief taxonomic schemes are given, with lists of species.

The systematic section opens with a table of "Classification" which adopts the opinions of Zittel published many years ago and which, in the main, seems to represent the facts as we now know them. Dissent has already been made as to the inclusion of the Diplocaulidæ in the order Microsauria to which group of vertebrates they have not the slightest relationship. The anatomy and relationships of the group have been discussed elsewhere[10] and it will only be necessary to state here that the structure, as we now know it, seems to point to a relationship of the Diplocaulidæ with the true Amphibia, *i. e.*, the Branchiosauria and the Caudata. A new order, Diplocaulia, has been erected for the reception of the species of the family. It is only proper to say that Dr. Case includes the Diplocaulidæ with the Microsauria provisionally. In the morphological section Dr. Case says (p. 90):

> Jaekel's suggestion of the derivation of *Diplocaulus* from forms like *Ceraterpeton* and *Diceratosaurus* is very probably correct.

He gives not the slightest reason for the assumption of the correctness of this view, which, in the light of the facts, can not be regarded as other than preposterous. The derivation of *Diplocaulus* from such differently organized animals as *Ceraterpeton* and *Diceratosaurus* is fully as fanciful as Jaekel's suggestion to Dr. Traquair of the probable descent of *Hunsrückia* "jene ältesten Fische von terrestrischen Tetrapoden abstammen."

[10] *Journal of Morphology*, XXIII, No. 1, March, 1912.

The section on the temnospondylous Amphibia is taken up with descriptions of the osteologic characters of the various species with little or no attempt at phylogenetic conclusions. This will make the present monograph the central point, a base of supply, from which future discussions must radiate. Dr. Case's work is reviewed more in detail by Mr. Mehl in *Science*, September 27, 1912, p. 408.

The second volume of Dr. Case's series of monographic studies on the American Permian vertebrates was issued October 25, 1911, as Publication No. 145 of the Carnegie Institution of Washington. In this volume Dr. Case has brought together all of the important facts concerning the "Cotylosauria of North America" with many notes on foreign genera. The volume has 121 pages, 14 plates, 52 text-figures and 71 bibliographic references. As in his previous volume on the "Pelycosauria" the author has divided this volume into the following sections: "Historical Review," "Classification," "Systematic Revision," "Morphological Revision" and "Conclusion."

The reptilian order Cotylosauria of Cope at present has assigned to it by paleontologists thirty genera, distributed in ten families and placed by Dr. Case in five suborders. Each species has the original description and a "revised description" so that later workers on these Permian reptiles will have at hand ready information concerning all the Cotylosauria known up to the end of the year 1911.

The members of the group are known mostly from fragmentary remains. Only in one case, that of *Diadectes phaseolinus* Cope, was the author able to restore the approximate skeleton of the species. Other forms have, however, been restored, notably, *Sclerosaurus* from Europe by von Huene, *Telerpeton* from Scotland by Boulenger, *Captorhinus* and *Seymouria* from Texas by Williston and *Labidosaurus* from Texas by Broili and Williston. Much still remains to be determined as to the structure of nearly all the species.

The facts of most general interest are the structure of the skull of these reptiles and the description of a brain cast of *Diadectes*, figured on Plate 7, Figs. 2 and 3. The structure of the skull allies the group with the stegocephalous Amphibia. The former notions of the Cotylosauria allied the group with the Stegocephala. Further study, however, has convinced Dr. Case that the group is "very far from occupying the primitive position assigned to it

by Cope." Possibly new discoveries of the appendicular skeleton will widen this gap and give us more definite ideas of the organization of what are possibly the most primitive of the known Reptilia. Similar ideas were formerly held as to the position of the mammalian order Condylarthra, but further knowledge of the anatomy of the skeleton of the body has convinced Dr. Matthew that the group has many characters which are not at all primitive and which would seem to remove the group from an ancestral position.

The Cotylosauria originated probably as early as the middle Pennsylvanic, although the evidence for this is uncertain. Two genera of reptile-like forms known from the Carboniferous of Ohio and France, *Eosauravus* Williston and *Sauravus* Thevenin, are doubtfully assigned to the order. If these are not Cotylosauria then the order is Permian. The Cotylosaurian reptiles have been found in America, Europe and Africa. There is little relationship existing between the faunas of the various continents and the place of origin of the order is uncertain, since representatives are found on both sides of the water at practically the same time geologically. This same thing is true among other fossil vertebrates, notably *Eohippus*, the Branchiosauria, the Microsauria, the Embolomeri, etc. The significant conclusion is reached that:

> There is no single one of the Cotylosauria that can be considered as an ancestral form of the other reptiles. . . . It is impossible to derive the Diapsidan and Synapsidan types from the known Cotylosaurs.

The make-up of the work is excellent. The figures are many of them new and all are well executed. The author has drawn on published matter to the Cotylosauria and has inserted figures from Cope, Broili, Williston, Boulenger, Moodie, Thevenin, von Huene and others, for all of which proper credit is given. The photographic plates are an especial desideratum, for while it leaves the exact description of the elements somewhat uncertain to the reader, yet one feels more at ease on seeing a photograph of the material. Most of the specimens described are in Walker Museum at the University of Chicago and the American Museum of Natural History in New York City.

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(*To be continued*)